ON THE STRUCTURE OF THE PTERASPIDÆ AND CEPHALASPIDÆ.

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I. THE fact which first suggested to me the possibility of a genetic relationship between the Vertebrata and Arthropoda was the similarity in structure and development between the median eyes of arthropods and the pineal eyes of vertebrates.

To test this idea a careful study of the brain, sense organs, cranial nerves, nephridia and skeletogenous structures was made, the results of which showed so clearly a fundamental similarity between the structure and the arrangement of these parts in the cephalothorax of certain arthropods and in the head of vertebrates, as to justify the conclusion that the vertebrates were derived from fully developed arthropod types, and that the solution of the various problems in the morphology of the vertebrate head must be sought for in the evolution of the arthropod cephalothorax.

For the advocate of the annelid theory of the origin of vertebrates, or of any other theory that assumes the vertebrates to be derived from soft bodied ancestors, an appeal to paleontology in support of anatomical or embryological evidence is well nigh hopeless. But for those who support the arthropod theory, such an appeal is imperative because paleontology is not likely to remain forever silent when both extremes of the series of hypothetical annectant types could be preserved as fossils.

The fossil forms that at first sight seemed most completely to bridge the gap between their respective types are the trilobites and Merostommata, representing the arthropods, and the ostracoderms representing the vertebrates. It seemed probable that a study of their remains, especially those of the ostracoderms, whose structure presents so many interesting problems, might furnish evidence for, or against, the supposed genetic relationship between these two groups. Moreover the fact that these ani-

mals are among the oldest representatives of their respective types known, that they were contemporaneous and lived under very similar conditions, and that they presented many obvious external resemblances in form and mode of life, clearly invited a more detailed comparison between them.

The evidence thus far obtained, justifies the belief that paleontology will add its evidence to that of anatomy and embryology in favor of the origin of vertebrates from arachnids.

From the following historical review it will be seen that while it is now generally assumed that the ostracoderms have pronounced affinities with the vertebrates, there is the greatest diversity of opinion among leading authorities as to whether certain organs characteristic of the true vertebrates are present in the ostracoderms or not, and there is also the greatest difference of opinion in the interpretation of those structures which are actually known to occur there. In many cases the despairing admission is made, that if certain openings, or structures, are not this, that, or the other, what can they be? This is not due entirely to the imperfect preservation of the remains, because in some cases they are beautifully preserved.

At the very outset, the obvious differences between the ostracoderms and true vertebrates, and the resemblance between them and the arthropods, was a subject for repeated comment. In fact the resemblance was so striking that it led many of the best earlier observers to describe certain merostomatous arthropods as fishes and various ostracoderms as arthropods. More recent authors while admitting that there is a superficial resemblance between these two great groups, explain this resemblance as one due merely to mimicry or parallelism, and not to a genetic relationship. Some authors even deny that the peculiar structure of the ostracoderms is an indication of their primitive character, but regard them as either highly specialized, or as degenerate offshoots from the class of typical fishes.

At first the discussion centered round the question whether certain genera of the ostracoderms, especially Cyathaspis and Pteraspis were arthropods or vertebrates. But whether or no these genera, and consequently the whole group of the ostraco-

derms, were annectant types uniting the true fishes with the arthropods, and possessing some of the characters of both classes, so far as I know, was not discussed by any writer till I raised the question in 1889, in my first paper "On the Origin of Vertebrates."

Huxley and Lankester answered the first question with great emphasis in favor of the vertebrates, basing their conclusions primarily on the microscopic structure of the head shields, the presence of fish-like scales in Pteraspis, and of a caudal fin in Cephalaspis. Their authoritative opinion settled the question for the time being, and soon afterwards, the almost universal belief in the derivation of vertebrates from soft bodied annelid ancestors that would leave little or no trace behind, and the wide-spread conviction that the growing science of embryology was to be the final court of appeal in all broad phylogenetic problems, turned the attention of morphologists away from the paleontological aspect of the problem.

The development of new lines of zoölogical research and the failure of embryology to realize the over confident expectations of its disciples, as well as the frequent and flagrant abuses of embryological data, have produced within the last decade a spirit of impatience, or of indifference, towards phylogenetic speculations in general and a reaction set in, not only against the annelid theory of the origin of vertebrates, but against all theories that attempt to bridge this, the widest gap in the whole organic kingdom, by a purely speculative use of embryological data.

The association of such names as Hugh Miller, Louis Agassiz, Huxley and Lankester with the early history of Pteraspis and the Cephalaspidæ adds greatly to the interest that has long centered in this group.

In *Siluria*, (London 1854, p. 252), Sir Roderick I. Murchison speaking of *Cephalaspis agassizii* says: "This fish with its large buckler-shaped head and its thin body, jointed somewhat like a lobster, is perhaps the most remarkable example of a fish of apparently so intermediate a character, that the detached portions of its head when first found were supposed to belong to Crustacea."

In a foot note Murchison adds: "Mr. Miller has requested his readers to compare the head of *Asaphus* (now *Phacops*) *caudatus*, a well-known Silurian trilobite, with that of *C. lyellii*, to illustrate how the two orders of Crustaceans and Fishes seem here to meet,—in the view of persons who have not mastered the subject."

Eichwald says ('54, p. 105): "It is very remarkable that this colossal crab (Pterygotus) formerly regarded by L. Agassiz as a fish .... occurs in the dolomitic chalk of Rootziküll in Oesel, together with another genus, Thyestes, standing between Crabs and Fishes and resembling Bunodes and Cephalaspis."

Hugh Miller, the discoverer of Pterichthys, says (*Old Red Sandstone*, p. 50), in comparing a trilobite with Cephalaspis "The fish and the Crustacean are wonderfully alike." .... "They exhibit the points, ... at which the plated fish is linked to the shelled Crustacean."

Sir Roderick Murchison, when first shown specimens of Pterichthys wrote regarding them that, "if not fishes, they more clearly approach to crustaceans than to any other class." Again, "They (Cephalaspis and Pterichthys) form the connecting links between crustaceans and fishes." Agassiz was at first in doubt as to whether Pterichthys was a fish or a crustacean.

The following quotation illustrates the attitude of modern paleontologists toward the ostracoderms. A. S. Woodward, whose opinion on this subject is entitled to the greatest respect, in his recent text-book of Paleontology ('98, p. 5) states that "Nearly all the genera (of the Ostracodermi) mimic in a curious manner the contemporaneous Eurypterids"; and on p. 24 of the Introduction, that "The oldest Ostracoderms .... sometimes claimed as the immediate allies of the crustacean or arachnid Merostomata of the same period, are fundamentally different from the latter in every character which admits of detailed comparison; they are to be regarded merely as an interesting example of mimetic resemblance between organisms of two different grades adapted to live in the same way and under precisely similar conditions."

Surely, no one knows either the precise conditions, under which these forms lived, or the "way" they lived. It would cer-

tainly be a very unusual thing if all the ostracoderms mimicked animals so different in grade of organization according to Woodward's view, as the Merostommata are. As a matter of fact, there is no more reason for assuming that the ostracoderms mimicked the Merostommata, than that the Merostommata mimicked the ostracoderms, and there would have been no obvious advantage to any of them on either supposition.

Moreover the features in which the ostracoderms mimicked the eurypterids are characteristic of a very extensive class and are the very characters which are important in differentiating the ostracoderms from the true fishes, such as, for example, the small pointed body, large shield-shaped head with its peculiar cornua, cephalic appendages, shell covered orbits, unusual character of the parts surrounding the mouth, and the minute structure of the nearly continuous dermal armor. It is the combination of all these characters that makes the resemblance between the ostracoderms and Merostommata difficult to understand on any other assumption than that of genetic relationship.

Clearly it is not convincing, or a final solution of the problem, to say that these extensive resemblances between two great classes of animals are due solely to either mimicry or parallelism.

II. The Pteraspidæ. Going back again to the older writers, we shall see that much of their discussion having any bearing on the position of the ostracoderms was on the structure and relations of the Pteraspidæ. But the fact that these animals were the first fish-like animals to appear on the earth's surface, and that they were found in some of the oldest fossiliferous rocks known, did not influence their views as to the nature of these forms so much as one might have supposed. Although certain parts of Pteraspis and Cyathaspis were at one time thought to be the bones of a cuttle fish, or the shields of trilobite-like crustaceans, a more careful study of their microscopic structure, and a comparison with related forms, showed that they belonged to a group of animals with unquestionable vertebrate affinities. This fact seems to have shut off all further consideration of their phylogenetic signification, for as soon as their vertebrate affinities were once established they were pigeon-holed

among the true fishes, and their existence practically ignored. Although the pteraspids are now generally placed among the true fishes, their head shields do not present a single recognizable vertebrate character. The various surface markings have been supposed to indicate the presence of median or lateral eyes, olfactory, or auditory, organs, or gill openings, or the impressions of gill pouches,— not because they show any particular resemblance to corresponding organs in true vertebrates, but because, as has been frequently said, there is nothing else with which they can be compared. There are no traces in these remains, which in general are fairly well preserved, of upper and lower jaws, fins, notochord, or vertebral column.

The genus Pteraspis was first proposed by Rudolph Kner in 1847 to include the forms described in 1835 by Agassiz as *Cephalaspis lewisii*, and *C. lloydii*. Their appearance was so unlike the ordinary fish remains that for a long time Kner did not suspect that they had been already described by Agassiz in his *Poissons Fossils*.

From a study of their minute structure Kner believed them to be the internal shells of cephalopods allied to Sepia.

In 1856, F. Roemer described a form closely related to *C. lloydii* as Palæoteuthis, and referred it to the Sepiidæ, but suggested that the forms described by Kner were crustaceans related to Dithyrocaris or Pterygotus.

In 1864, Lankester divided the Pteraspidæ into the three genera, Pteraspis, Cyathaspis and Scaphaspis. But in 1872, Kunth described a shield of Cyathaspis, below which he found one belonging to Lankester's genus Scaphaspis, and he rightly concluded that the two shields belonged to the same animal. He maintained that the lower shield bore the same relation to the upper one that the tail plate of a rolled up trilobite does to its head shield, and that between the two were a number of pieces comparable with the segmental trunk plates of a trilobite. Other plates were present which Kunth regarded as locomotor organs, or foot-jaws. From the above facts Kunth concluded that these remains were not those of a fish but of an arthropod. In referring to Huxley's statement that there is no molluscan or crustacean structure with which such remains could be for a moment

confounded, and to Kner's belief that Scaphaspis was the shell of *Sepia officinalis*, Kunth adds "so schienen mir diese Ansichten in verein mit unserem vorliegenden Stücks mir zu beweisen dass wir es mit einer Crustacean Abtheilung von ganz eigenthümlicher Schalstructur zu thun haben. Denn jedenfalls giebt es weder einen Fisch noch eine Sepien Schulpe, die eine ähnliche Structur wie die Schilder zeigte; wohl aber ist die Organization des ganzen Stückes beweisend fur Crustaceen Character" (p. 6).

Both Schmidt ('73, p. 330) and von Alth (p. 47) agree with Kunth that Scaphaspis is the ventral shield of Pteraspis, but they deny that any of the remains described as Pteraspis, Cyathaspis or Scaphaspis are crustaceans, although no valid reasons are given for doing so.

Huxley ('58, p. 277) in reply to Agassiz, who had remarked on the singular resemblance between the shell of *C. lloydii* and that of crustaceans, and to Roemer's and Kunth's opinion that Pteraspis was a crustacean, seems to have closed the discussion for the time with his oft quoted statement that "No one can, I think, hesitate in placing Pteraspis among Fishes. So far from its structure having 'no parallel among fishes,' it has absolutely no parallel in any other division of the animal kingdom. I have never seen any molluscan or crustacean structure with which it could be for a moment confounded."

Roemer accepts these statements apparently because they came from Huxley, although he does not make an unconditional surrender of his opinion, for he says "Allerdings manche Analogie der aüsseren Form mit Crustacean-Formen dar bieten wurde."

In 1855, R. W. Banks in his paper on the Downton Sandstones, after commenting on the association in these beds of *Lingula cornea*, Pterygotus and Pteraspis (Cyathaspis), made the following observation, p. 98, "On the under side of the sharp projections before referred to (on either side of the rounded snout) are protuberances which seem to be projecting horny eyes similar to those of Crustaceans."

He remarks further on, that doubtful as it is whether the buckler-like fossil remains above referred to belong to fishes or to crustaceans, it is certain that they are closely allied to *Cepha-*

laspis lloydii and *C. lewisii*. In a final note, it is announced that Professor Huxley is now minutely examining their structure to determine their true relationship either to the crustaceans or to the fishes. When Huxley's paper appeared, although he gave a very good description of the minute structure of the shell of these animals and concluded that they are not crustaceans, he entirely ignored the existence of the eye tubercles, although their presence afforded very weighty evidence against his conclusion.

Lankester ('68, p. 26) admitted the presence in Cyathaspis of tubercles corresponding with similar tubercles in Pteraspis, which are "produced by the supposed orbits"; but how a vertebrate eye, or an "orbit," could be preserved as a beautifully rounded protuberance when all the other soft parts are completely destroyed, is not discussed.

Lankester however, ('73, p. 241), still maintained the validity of his genera Scaphaspis and, in another article ('73, p. 190) makes the following statement: "It is to me a source of twofold regret that Dr. Kunth has perished in the Franco-Prussian war, for not only have we thus lost a chance of obtaining additional knowledge of the Berlin Cyathaspis, but I shall be unable to obtain from him the admission that his conclusion is not in accordance with the facts." Lankester ('91) finally admits that von Allth's discovery shows Scaphaspis to be the ventral shield of Pteraspis, and thus we may assume that his "twofold regret" for Kunth's untimely death was in a measure mitigated.

Lankester attaches much importance to the presence of scales on the anterior trunk region of Pteraspis, for these scale-like structures are regarded as conclusive proof that the Pteraspidæ belong to the vertebrates. As Lankester says ('68, p. 18) "All that is known as regards the scales of these Fishes is from a single specimen found in the Cornstones of Herefordshire." This specimen, he says elsewhere ('73, p. 191) "Shows seven rows of rhomboidal scales attached (not merely adjacent to) to a portion of the head shield of Pteraspis. That these are true scales, or lozenges of sculptured calcareous matter is absolutely certain. It is also absolutely certain that the shield is pteraspidian and that the scales and shield belong to the same individ-

ual organism. The scales are fish-like. I know no Arthropod, nor any other organism except a fish which possesses any structure even remotely representing them." "The shields of the Chitonidæ and Cerripedæ are the only animal structures, except the scales of a ganoid fish (with which they agree exactly) which they could even vaguely suggest." "The form of this shield, and its details as to apertures, processes, etc., agrees with the view that it belongs to a fish most fully. It has not the remotest suggestion of Crustacean affinities about it."

After commenting on the fact that the fossil in question was marked with long parallel striæ, and that the middle layer contained the polygonal cavities he adds ('64, p. 195), "This structure, which has no parallel among fishes, or, indeed, any group of the animal kingdom, leaves no possibility of a doubt that the specimen is a fragment of Pteraspis." . . . . Lankester further maintains ('68, p. 4) that by the discovery of these scales "the piscine nature of these fossils was definitely set at rest."

These positive statements are somewhat contradictory and would now be hardly warranted by the facts of the case. The crustacean character of the shields has been repeatedly commented on by competent observers. In his own monograph (p. 61) he has described a fragment, possibly connected with Cephalaspis which he names *Kallostrakon podura* (Tolypelepis ?) "on account of the resemblance to the well-known microscopic markings of the scales of the insect Podura."

It is not true that there are no arthropods with structures even remotely resembling these scales, because in Pterygotus the entire body is covered with an ornamentation which bears an astonishing resemblance to fish scales, so much so as to deceive such a keen observer of fishes as Louis Agassiz. Moreover in many trilobites and in the Ceratiocarina, Clarke, the surface of the shell is ornamented with ridges and grooves not unlike those of Pteraspis in external appearance.

Lankester probably would not have made these statements had he kept Pterygotus in mind, or had he been acquainted with the minute structure of the shield of Limulus.

Moreover all recent students of the shell of Pteraspis are agreed that it is *not* "exactly" like that of a ganoid fish, in fact its microscopic structure is altogether of a different character.

But after all, the presence or absence of these scales in Pteraspis has little weight, it seems to me, in answering the real question at issue, namely whether Pteraspis in addition to its vertebrate affinities has not also a genetic relationship with the arthropods.

Lankester, Woodward, Traquair, Rohon and others agree in denying the existence of arthropod characters to the pteraspids, apparently because of the abundant evidence now available that Pteraspis is related to Cephalaspis whose ichthyic affinities have rarely been questioned, rather than because the arthropod features of Pteraspis have been dispassionately considered and found wanting.

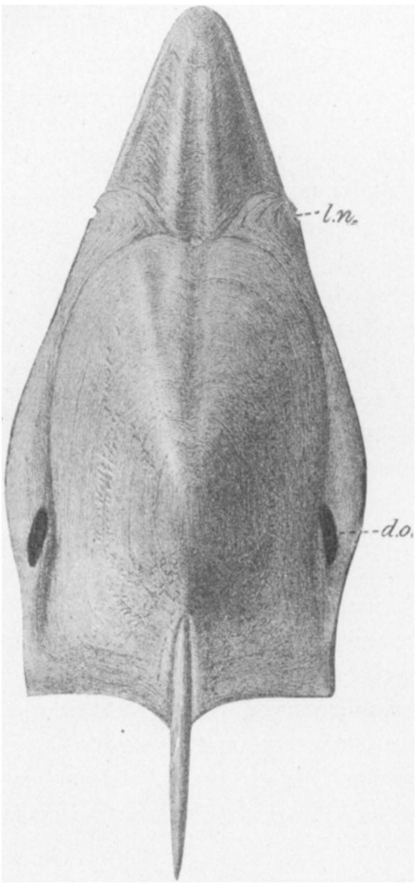


FIG. 1.—Cephalic buckler of Pteraspis, dorsal view, after Lankester. The shape of the lateral openings, *d. o.* has been slightly modified; *l. n.* the supposed lateral eye openings, possibly, the points for attachment of appendages.

But within recent years there seems to be a growing tendency to doubt the affinity between Pteraspis and Cephalaspis. Reis protests against their union, and apparently Traquair is in doubt, treating them together largely as a matter of convenience. Lankester in his earlier monograph states that "The Heterostraci are associated at present with the Osteostraci because they are found in the same beds, because they have like

Cephalaspis a large head shield, and because there is nothing else with which to associate them." More recently he has said ('97) "There is absolutely no reason for regarding Cephalaspis as allied to Pteraspis, beyond that the two genera occur in the same rocks, and still less for concluding that either has any

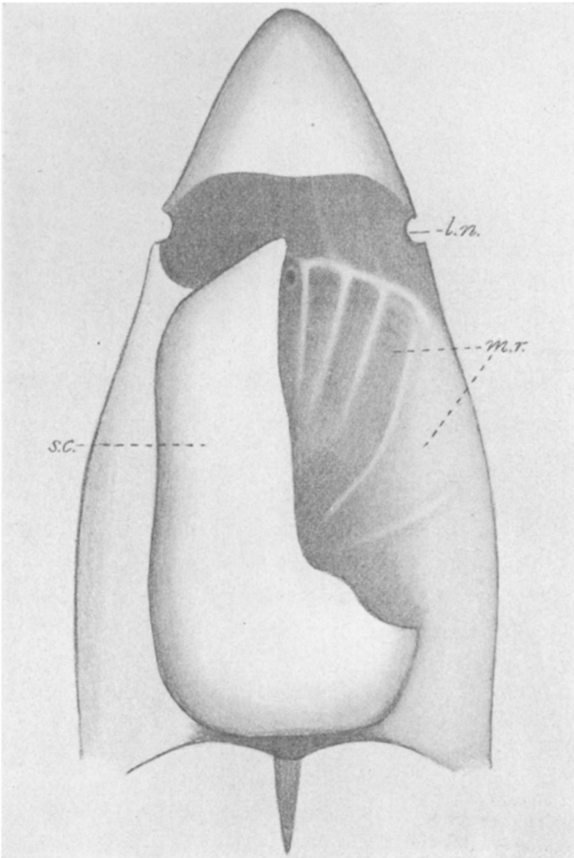


FIG. 2.—Cephalic buckler of Pteraspis, ventral view, showing the small oral region, probably filled with several pairs of plates. The large ventral plate, *s. c.* is supposed to be cut away on one side showing the median eye pit and the paired muscle markings of the inner surface of the dorsal shield.

connection with Pterichthys." Zittel says, Vol. III, p. 147, "Mir scheinen die Beziehungen der Pteraspiden und Cephalaspiden nach Form und Structur so entfernt dass beide besser als

besondere Ordnungen betrachtet werden." He remarks further on that while the Cephalaspidæ certainly appear to be ganoids, the position of the Pteraspidæ is very doubtful.

It seems to me that there can no longer be any doubt on these points, since the Pteraspidæ and Tremataspidæ are pretty closely united with the Asterolepidæ by the similarity of their oar-like appendages, and with the Cephalaspidæ, by the similarity of the median and lateral openings in Tremataspis, Thyestes and Cephalaspis.

At present, of the genus Pteraspis, only a part of the cephalic armor and a few scale-like structures belonging to the anterior part of the trunk, are known. The head, Figs. 1 and 2, is arrow shaped and covered by a dorsal and ventral shield, the latter, the so-called Scaphaspis, consisting of a single ovate or oblong piece, varying in different species from $1\frac{1}{2}$ to $3\frac{1}{2}$ in. in length.

The lateral edges of the ventral shield probably fitted closely to the lateral edges of the dorsal one, leaving under the rostrum a comparatively small opening in which the various mouth parts were situated.

The boat-shaped dorsal shield is composed of seven portions, marked off on the outer surface of the shield by furrows, and on the inner surface by ridges. In young specimens, the rostrum and the central disc may be found separately. Each piece has its surface ornamentation of ridges and furrows arranged in concentric lines parallel with its margins. This fact, together with other considerations, led Lankester to believe that each piece ossified from a separate centre and that their complete anchylosis occurred only in the adult.

Muscle Markings.—In 1872, A. Kunth described in *Cyathaspis integer* a series of six "flache Höcher," situated on the under surface of the dorsal shield, which he regarded as indications of segmentation, Fig. 4. Lankester, ('73), describes similar impressions on the shield of *Cyathaspis banksii* and believes that in both cases they indicate the position of a series of branchial chambers.

In Pteraspis also, Lankaster has described five narrow ridges, with four broad shallow depressions between them, which radiate

from the centre of the inner surface of the dorsal shield, Fig. 2, *m. r.* They are perhaps best marked in *Pteraspis crouchii* and *P. rostratus.*

These markings on the dorsal shield of the Pteraspidæ are, I believe, best explained as indications of the original segmentation of the head, produced in part by the attachment of strong segmental muscles extending vertically from the inner surface of the dorsal shield, either to a cartilaginous cranium, or to a series of gill-like or jaw-like segmental appendages on the ventral side. They suggest the markings produced in this manner on the dorsal surface of the cephalothorax of Limulus, or the lobulations on the dorsal shield of a trilobite head.[1]

Eyes.— There is a conspicuous pit on the inner surface of the shield, appearing on the outer surface as a small tubercle, which marks the position of the median eyes.

Lankester ('70) shows in his Fig. 6, Pl. IV, three tubercles near the median anterior part of the head of Cyathaspis, and the same tubercles were figured by A. Kunth in 1872. In both figures, the resemblance of the shields to the cephalothorax of an arthropod is intensified by the shape and arrangement of these three ocelli-like tubercles (Fig. 4).

The location of the lateral eyes of Pteraspis is supposed to be indicated by two smooth tubercles, or in some cases by circular openings, near the anterior margin of the shield, *l. n.* It is hard to understand how the usual type of vertebrate eye could be preserved in the form of these tubercles. If they are lateral eye tubercles, they, like the compound eyes of arthropods, must have been enclosed by a firm dome-like covering, continuous with the outer layers of the shell. I have never seen any specimen of Pteraspis in which these so-called lateral eye notches were actually covered by an extension of the outer shell layer, although such a covering is found over the large median eyes of Cephalaspis and Tremataspis. It is possible that there are two pairs of such notches, or openings, in Pteraspis, Cyathaspis and Tolypelepis, one serving for the lateral eyes and the other for the attachment of swimming appendages similar to those of Tremataspis.

[1] Rohon has described a somewhat similar segmentation of the head in Thyestes.

The projections sometimes seen in the so-called orbital notches of Pteraspis, appear to be the remnants of appendages.

Dorso lateral openings.— In Pteraspis a large oval opening on each side of the dorsal shield leads into a wide canal that runs diagonally forward and downward into the interior of the head (Figs. 1 and 3, *d. o.*). Lankester ('68, p. 17) says, "It is very difficult to find any explanation of these open excavated structures unless they be spiracles."

Although the margins of these openings are not well enough preserved to show such important details as are seen in Tremataspis, their shape and position indicate that they may be homologous with the lateral openings in the dorsal shield of Cephalaspis, Thyestis and Tremataspis. Like the openings in the shields of these three genera, they were probably covered by an extension of the outer shell layer, possibly by loosely fitting polygonal plates. This may be the reason why Claypole, (p. 566), found no trace of such openings in Palæaspis.

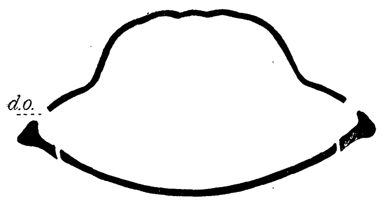


FIG. 3.— Cross section through the posterior portion of the cephalic buckler of Pteraspis. The section of the dorsal shield with its lateral openings is from an actual section. The ventral shield is restored.

Sections of two different specimens (Fig. 3) show that there is no extension of the inner layers of the shell over the opening, like that seen in Tremataspis and Cephalaspis.

If this interpretation of the lateral openings in Pteraspis is accepted, there is no reason for supposing that they have anything to do with the gills, and the argument that Pteraspis is a fish because it has spiracles, or gill openings, is eliminated.

Appendages.— In *Palæaspis americana*, Claypole ('92, p. 554), finds indications of appendages consisting of small objects resembling spines "margined with what appeared to be a flat fringe around their smaller and pointed ends; .... the central spine-like portion was covered with a layer of the same tissue as that of which the shield was composed." He then adds that the resemblance of the structure to a crossopterygian fin was obvious. "Two forms of fins appear to prevail, the one broad and

the other narrow, indicating that more than one pair belonged to the same individual."

These facts are of great significance in view of Lindström's discovery of the appendages in Cyathaspis, (Fig. 4) and of my own discovery of appendages in Trematas-pis. Dean ('95, p. 71) maintains that the structures in question do not have the significance claimed for them by Claypole, and that they do not even belong to Palæaspis but to some elasmobranch. But Claypole's observations seem to have been made with great care, and in view of the importance that must be attached to them, if confirmed, they deserve more careful consideration than they have heretofore received.

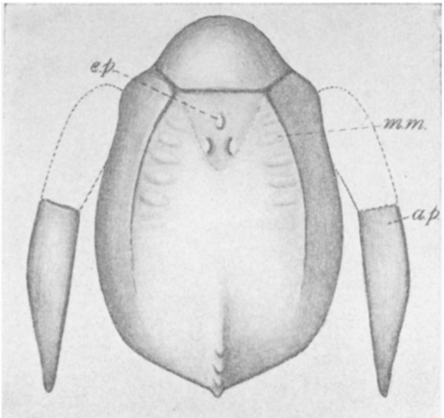
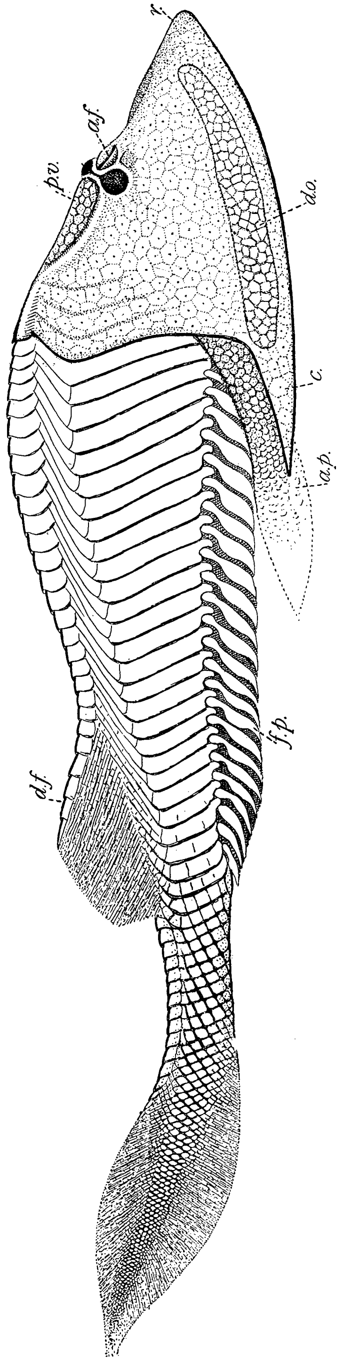


FIG. 4.—Restoration of the head shield of Cyathaspis, showing the oar-like appendages, *ap.* the three median eye pits, *ep.* and the paired muscle markings, *m. m.* sometimes regarded as the impressions of gill pouches. The eye pits and muscle markings are best seen in casts of the inner surface.

III. THE CEPHALASPIDÆ are found in the upper Silurian and in the Devonian formations, and range in size from a few inches to possibly two feet or more in length.

Shape of Head.— In Cephalaspis, (Figs. 5 and 6), the typical genus of the family, the head was completely enclosed in a continuous cephalic buckler or shield, which seen from above is elipsoidal in outline, either rounded or pointed in front and truncated behind. The lateral angles of the posterior margin extend backwards to form the cornua, while the median posterior portion forms a broad crest often armed with a prominent median spine.

Cross sections (Fig. 8 *B*) show that the head is thin and



spoon-shaped, with its concave surface facing downwards. It rests on a flat, thick-walled rim which gradually widens posteriorly till it forms the under side of the broad triangular cornua. The ventral wall of the shield is thin, and is pressed closely against the dorsal wall. Toward the middle line it is gradually reduced to a flexible membrane which terminates abruptly, leaving a large median opening in which the soft parts of the head were situated.

Eyes.— Near the middle of the dorsal surface are the oval openings for the eyes. Cross sections of the orbits, and fragmentary casts of their outer surface, show that the eyes were nearly spherical, and that they projected dome-like above the surface of the head. They were covered by a thin coating of hard material continuous with the outer layer of the shield. The floor of the orbits is very concave and consists of a basket work of bony trabeculæ formed by an extension of the inner shell layer.

FIG. 5.— Restoration of Cephalaspis, seen from the side; no attempt has been made to indicate specific differences; *a. p.* cephalic appendages, so-called "opercular flaps," *c*, cornua; *d. o.* marginal organs; *r.* rostrum; *a. f* ant-orbital fossæ with median perforation; *e.* eyes; *p. v.* post-orbital valley; *d. f.* dorsal fin; *f. p.* fringing processes.

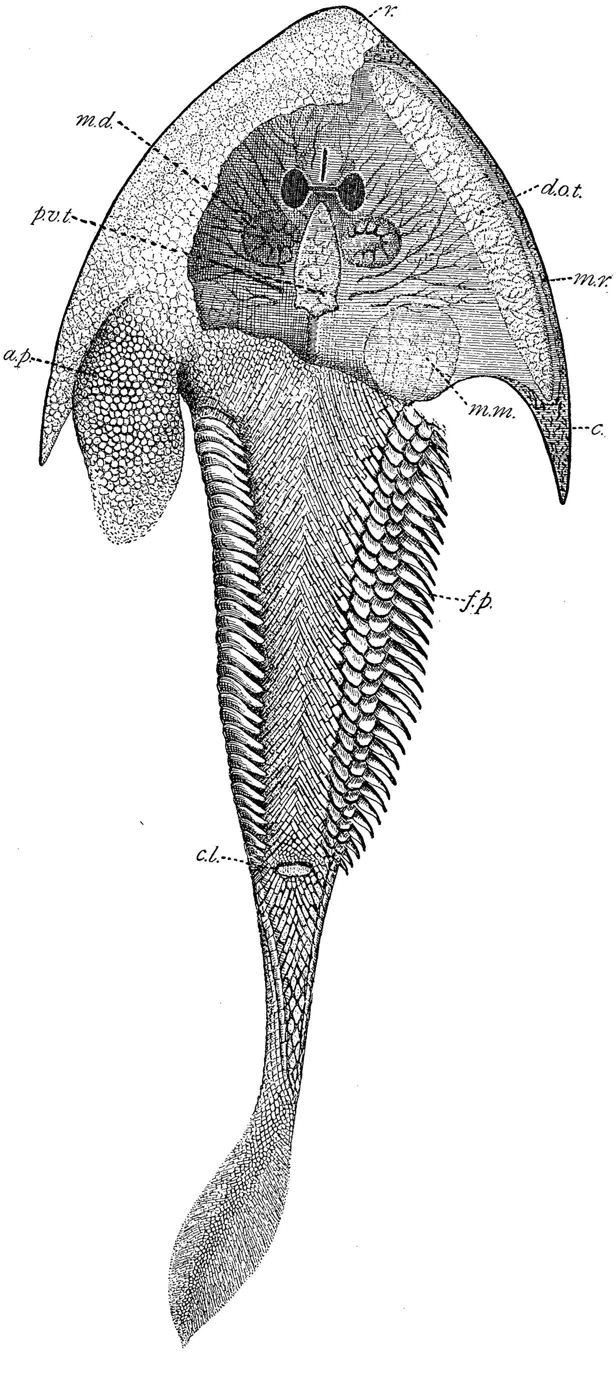


Fig. 6.—Restoration of Cephalaspis, seen from below. A part of the ventral wall of the head is shown on the left, the rest is removed, showing inner surface of the roof of the shield; *m. r.* net work of osseous trabeculæ supporting the margins of the shield; *d. o. t.* mass of bony tissue forming the floor to the lateral openings; *p. v. t.* same kind of tissue below the post-orbital valley; *m. m.* large muscle scar; *f. p.* fringing processes, extended on right, and folded on to abdomen on left; *cl.* cloacal opening. Other letters as in Fig. 5.

The eyes, therefore, of Cephalaspis, like those of Tremataspis and Bothriolepis were imbedded between two layers of the dermal armor, and in this respect agree with the condition which prevails in both the median and the lateral eyes of Limulus (Fig. 8 *A*).

Two depressions lie just in front of the orbits (the so-called ant-orbital fossæ (*a. f.*). They are separated by a median crest,

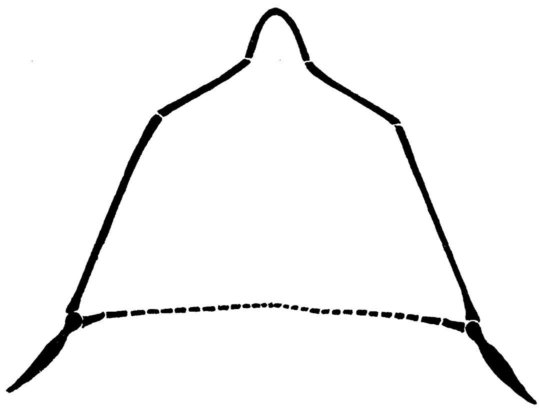


FIG. 7.— Diagrammatic cross section of trunk of Cephalaspis.

the summit of which is perforated by a narrow slit which leads into the interior of the head.

On the inner surface of the shield, near the lateral margins, are two very large oblong thickenings composed of a net-work of osseous trabeculæ (Pl. I, Figs. 2, 3 and 4, and text figs., 5 and 6, *d. o.*). Another prominent mass of the same tissue lies in the median line, just behind the orbits and just beneath the post-orbital valley (*p. v.*).

These lateral thickenings have been obscurely indicated in some of Lankester's figures, but I can find no reference to them in the text. They are probably the "pair of great rounded lobes meeting in the middle line" mentioned by Woodward (p. 179, Part II), and the "pouch-like sensory organs" of Dean ('95, p. 67).

In the specimens here figured the lateral lobes do not meet in the median line and I have not seen any specimens in which they do. When the outer surface of the shield is preserved, it

shows a well defined opening corresponding in position and outline with the mass of trabeculæ below. In some specimens, the opening is covered by a special group of loose, irregular polygonal plates, well shown in Pl. I. Fig. 3.

The mass of trabeculæ below the post-orbital valley is conspicuous and is often very sharply outlined (Pl. I. Fig. 2). It is oblong, pointed in front, and broad and somewhat angular behind.

The post-orbital valley when seen from above, in well preserved specimens, presents a clearly defined oblong opening, similar in shape to the underlying mass of trabeculæ, and filled with polygonal plates similar to those of the marginal openings.

In Thyestis, Fig. 9, I have found marginal and post-orbital

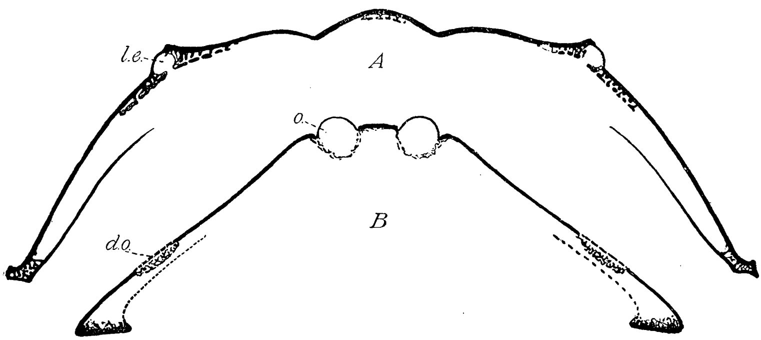


FIG. 8.—A. — Cross section of the cephalothorax of Limulus, showing arrangement of the bony trabeculæ in the median line, below lateral eyes and on the margins of the shield. The section is too far back to show the trabeculæ below the median eyes. B.— Cross section through the head of Cephalaspis, showing orbits, lateral organs, and part of the ventral shield.

openings similar to those of Cephalaspis, but smaller and more like those of Tremataspis. The covering polygonal plates, however, are absent.

There can be no doubt that the marginal and post-orbital openings of Cephalaspis and Thyestis, and perhaps the marginal openings of Pteraspis, are the same as those so well shown in Tremataspis, and that in all these genera some important organ of a sensory nature was lodged between the two layers of the shield at these points. I have shown that the arrangement of the marginal openings in Tremataspis is very suggestive of that of the lateral eyes and dorsal organs of Limulus (:01, p. 7).

The marginal cells of Eukeraspis Lank., seem to be a special development of bony trabeculæ similar to those below the lateral openings, but more loosely arranged. They serve to unite the dorsal and ventral laminæ, and to give additional strength to the rim of the shield.

I have already pointed out (:01), that in Limulus there is a system of supporting bony trabeculæ similar in structure and arrangement to those in Cephalaspis. In Limulus, as in Cepha-

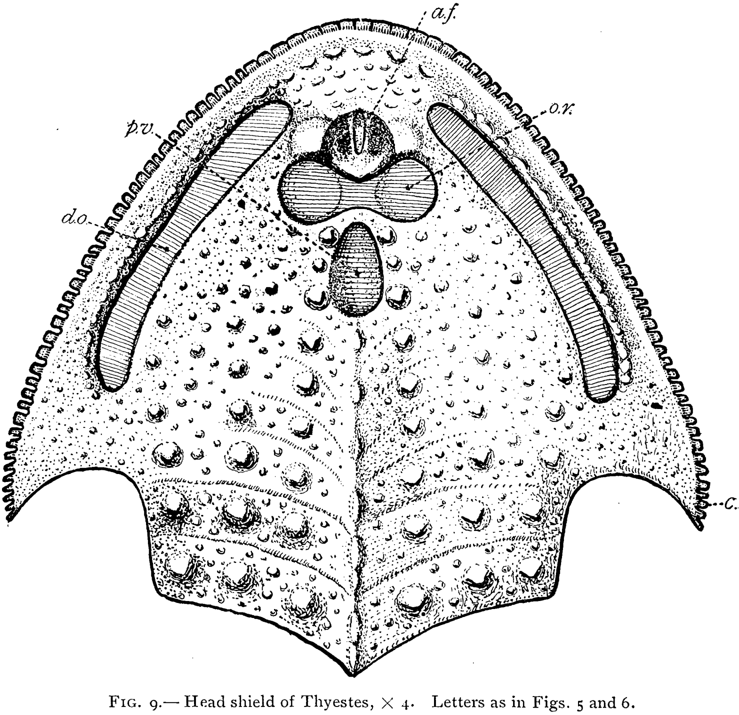


FIG. 9.— Head shield of Thyestes, × 4. Letters as in Figs. 5 and 6.

laspis, the principal masses of the trabeculæ lie along the margins of the shield, in the cornua, and beneath the median and lateral eyes.

Trunk Scales and Fins.— The dorsal surface of the trunk is covered with a single row of saddle-shaped, overlapping scales, sometimes fused into larger groups. The ridge scales extend on to, and support, the anterior margin of the dorsal fin, which appears to be merely an expansion of the dorsal ridge.

The dorsal fin must have been nearly immovable, as it is sheathed with parallel rows of oblong scales which diminish in size toward the free margin. The tail lobe is covered by similar scales. It was diphycercle, not, as is usually stated, heterocercle. In some cases I have seen indications that it terminated in a long, banner-like filament.

The flanks are covered by two principal rows of scales, the dorso-lateral one consisting of plates placed at a sharp angle with the dorsal crest, and in some cases twice as numerous as the crest scales (Pl. II, Fig. 7). The posterior edge of each scale overlaps the anterior edge of the next following one.

The lateral trunk plates are much larger, and stand nearly vertical. There is a semicircular incision on the posterior angle of the ventral end of each scale, into which fits the head of the fringing processes. The scales begin to break up into irregular polygonal plates about opposite the cloaca (Pl. II. Fig. 6, and text Fig. 5).

The ventral surface of *Cephalaspis murchisoni* is flat and triangular in contour. It widens out towards the ventral surface of the head, and narrows toward a point a little distance behind the cloaca. Its lateral boundaries are sharply defined by the projecting fringing processes. It is covered with small scales arranged in well defined rows, directed from either side diagonally inwards and forwards (Pl. II, Fig. 5). In *Cephalaspis lyelli*, they are directed backwards.

The outermost ones of the ventral scales appear to be nearly square and in some places (Fig. 6) present a distinct joint for the articulation of the fringing processes. Next to them comes a rather large oblong plate. The remaining scales in each row diminish in width as they approach the median line, where they are sometimes curiously crossed as though formed by imbricating filaments.

Cloaca.— In one beautiful, heretofore undescribed specimen in the British Museum (P. 8804 ?) about two thirds of the distance from the anterior end of the trunk, there is a well defined transverse slit that no doubt represents the cloaca (Pl. II, Fig. 5). Its posterior lip is smooth and rounded, the anterior one is more sharply defined, and forms the basal line of a triangular area covered with minute rhomboidal scales.

Back of the cloaca, the scales are arranged in obscure V-shaped rows, gradually breaking up into the squarish plates seen on the sides and ventral surface of the root of the tail.

Mandibles.— In my paper before the Fifth International Congress at Berlin, I referred to the presence of certain problematical structures in the head of Cephalaspis. I stated that my attention was first called to this subject several years ago by one of Lankester's figures (Pl. X, Fig. 2) which seemed to suggest the possibility of some kind of appendages on the under side of the shield, in the mouth region. Lankester made no reference in the text to the structure in question. On examining this specimen in the Edinburgh Museum of Arts and Sciences (No. 182), two oval bodies were found, lying in about the middle of the under side of the shield, just back of the orbits, and conspicuous on account of their peculiar shape and smooth shining surface.

Each body had a smooth under surface with fluted sides. Their symmetrical form and arrangement shows beyond doubt that they formed an organic part of the head.

The muscles moving these structures at first appeared to be attached to the large, circular, muscle scar on the inner surface of the dorsal shield, between the cornua and the posterior part of the dorsal crest (Fig. 5, *m. m.*) but I am now inclined to believe these marks were made by muscles moving the so-called opercula.

It is extremely probable that similar mouth parts occur in other ostracoderms. In Tremataspis, I have shown that the oral plates so completely fill the opening in this region that there is little room for the presence or action of upper and lower jaws of the vertebrate type. The shape and arrangement of these plates indicate that the large anterior pair in Tremataspis represent the mandibles which like those of the arthropod type must have moved to and from the median line when in use.

In Bothriolepis, we see even more clearly, as we shall describe in more detail elsewhere, that the so-called mental plates were mandibles of this kind. They are the only pair of plates present that could serve as jaws, and their general contour, the long

muscle ridge on their inner surface and the thickened, inturned median ends, that were probably armed with chitinous, or horny sheaths, show that they acted against one another in the median line, either as cutting, or crushing jaws. Their structure and position show in the clearest manner that the mouth must have been situated *between* these mandible-like plates, not in front of them. The presence of these remarkable structures around the mouth of the ostracoderms shows more clearly perhaps than anything else how wide the gap is between them and the true fishes.

Appendages.— Powrie was the first to call attention to the paddle-shaped lappets, or so-called pectoral appendages of Cephalaspis. They were later described and figured by Lankester and Powrie as "Ellipsoidal expanses with some calcareous matter in their structure which has caused them to be preserved." They are characterized by a kind of reticulate or areolate marking and although they show no trace of fin rays, they were regarded as a remarkable kind of pectoral fin, "efficient in causing currents of water to pass to the branchial organs."

Woodward has more recently examined some well preserved specimens of *C. murchisonii* and makes the following statement in regard to them: (Cat. B. Museum, p. 186). "A novel point of much general interest is elucidated by the middle layer of the shield, which is well preserved in several specimens." "The present specimens prove distinctly that it extends backwards as a pair of postero-lateral 'flaps' beyond the rest of the shield." "The outer layer is broken away, so that direct continuity can be observed between the appendage and the middle layer." "The structures are merely a portion of the shield itself, divested of the outer and inner layers to insure flexibility" (p. 187).

After quoting Lankester's opinion of them, he adds, "Some connection with the gills has thus already been suspected and it now seems most probable that the appendages in question actually correspond to a pair of opercula, and may henceforth be designated as such."

I have studied these appendages in the collections of the

British Museum and those at Edinburgh, but could find no evidence that the folds are formed as extensions of the middle layer of the shield. They appear to me to be covered by the usual shell layers, but broken into small shell-like plates united in such a manner as to allow some flexibility to the whole structure. They are not in my opinion specializations of the posterior lateral margin of the cephalic shield, or of the cornua, but true appendages attached to the under side of the head. The large circular muscle scars seen on the inner surface of the dorsal shield (Fig. 5, *m. m.*) probably served for the attachment of muscles moving these appendages.

I cannot agree with Woodward and Lankester in regarding these structures as opercula, for sections indicate that the sides of the head were very thin, and that the most important cranial organs were near the median line. Hence the so-called opercula, standing so far back, and to one side, and when the animal was at rest lying flat-wise against the bottom, were not in a position to cover the gills, or to produce currents of water through them.

Traquair regards the lappet-like flaps of the Cœlolepidæ as pectoral fins. These "lappets" it seems to me are represented in the Cephalaspidæ, by the cornua. Traquair's position is a difficult one to maintain, in that it compels him to look on the cornua of Drepanaspis as fins "rendered utterly functionless as fins by being enclosed in unyielding bony plates" (p. 846).

The true interpretation is to be obtained, I believe, by reversing this order of events and assuming that the ridged cornua of forms like Cephalaspis, Pteraspis, Drepanaspis, and others, are homologous and the most primitive because they are most like the cornua of their arthropodan ancestors. It is well known that cornua like those of Cephalaspis are present in many trilobites, and that in Limulus the two walls of the cornua are united by bony trabeculæ produced by an elaborate development of the inner shell layers, and suggestive of the reticulated structures filling up the cornua of Cephalaspis.

According to Dean, ('95, p. 69) the large oar-like appendages of Pterichthys are "lateral head angles produced and specialized" for locomotion.

If it is so easy in this instance to create *de novo* highly

specialized appendages like those of Pterichthys, with their necessarily complex arrangement of muscles and nerves, then the elaborate discussions over the origin of the paired appendages of higher vertebrates would seem to be a waste of time. But some such explanation as that offered by Dean is forced on those who regard these animals as true fishes by the difficulty, from their point of view, in explaining the presence of so many different kinds of appendages in a vertebrate head, for it is generally assumed that the appendages of Pterichthys are not homologous with those of Cephalaspis, and that neither one nor the other are homologous with true pectoral fins.[1]

The Fringing Processes. — Lankester showed long ago, in his reconstruction of Cephalaspis, a fringe of peculiar plates along the ventral margins of the trunk, which, although they produced a most unusual appearance, have not attracted the attention they deserve. Whatever their significance may be, there is apparently nothing known in true fishes that is exactly comparable with them.

In one specimen belonging to the Powrie collection in the Edinburgh Museum (No. 163) the body was badly crushed, throwing the plates to one side where they lay flatwise and well separated. On examination with a lens, some of the plates appeared to consist of at least two joints, possibly three, the distal one being the smallest. The surfaces of the plates were covered with coarse spines. The details of this specimen were not brought out by the photographs with sufficient clearness to allow them to be reproduced.

In the beautiful Ledbury specimens of *Cephalaspis murchisoni*, described by Woodward, the fringes are clearly seen in various positions, either from the sides or from below (Pl. I, Figs. 1 and 5.) In most cases they form a series of regularly overlapping, oblong plates, apparently in their normal position on the ventral margin of the trunk. Each plate appears to be three lobed, the segmentation being indicated by the gently rounded outline of each joint, as well as by the transverse lines that separate one

[1] Jaeckel (:02, p. 111) regards the "opercular flaps" of Cephalaspis as homologous with the dermal skeleton of a crossopterygian pectoral fin.

joint from the other. The mode of articulation with the body scales is not shown by any specimens of this species examined.

In the magnificent specimen originally described by Agassiz, (Pl. II, Fig. 6) the animal lies at full length in a natural position. Here the fringing processes are seen edgewise, and have a different shape and appearance from those of *Cephalaspis murchisoni*. They hang freely away from the trunk, in a nearly vertical position, with their distal ends bending backwards in graceful curves. Each process has a rounded head that fits into a cup-like depression on the posterior ventral margin of the large dorso-lateral trunk scales. Below the rounded head, the process is at first quite slender, then somewhat abruptly thickened, and finally reduced to a thin lamella with indistinct boundaries. There are from twenty to thirty pairs, beginning just back of the cephalic shield and gradually decreasing in size from that point toward the tail end. The most posterior ones are reduced to mere spines, or rhomboidal plates, loosely articulated to the lateral trunk scales.

Finally in a small specimen in the Powrie collection at Edinburgh (No. 139), where the whole animal is seen in outline from below, the fringing processes of both sides are shown folded inwards and flattened against the ventral wall of the body (Fig. 10). On the left side of the figure, one can count about twenty processes.

The varying appearance of the processes is due in part to their position and to the way in which they are exposed, and in part to the fact that the plates belonging to different species differ considerably in structure.

In *Cephalaspis murchisoni*, the fringe plates are lobed and overlap one another so that their flattened surfaces are directed diagonally forward and outward. In *Cephalaspis pagei*, they appear to have a similar shape and arrangement, but are armed with coarse projecting spines that give them a decidedly arthropod appearance. In *Cephalaspis lyellii*, the plates lie one directly behind the other without overlapping, while the prominent articulating head, the narrow neck, the posterior swelling and the thin, backwardly directed distal ends give them a unique and characteristic appearance.

FIG. 10.—Small specimen of Cephalaspis seen from below. It shows on the left the fringing plates folded over on to the abdomen.

There can be no doubt that the fringing processes projected freely from the ventral margin, and that they were freely movable forward and backward, and to and from the median line.

The conditions we have described are not less extraordinary than the fact that such conspicuous structures should have remained so long practically unnoticed. Lankester does not discuss their possible signification in his text, but merely introduces them into a very diagrammatic cross section as plates protruding like bilge keels away from the body. Many of the newer specimens of *Cephalaspis murchisoni* in the British Museum, as well as some of the older type specimens, show in the clearest manner that the fringing processes are articulated to the ventral margins of the body and are not artificial folds made by pressing together the margins of the dorsal and ventral walls (Fig. 7).

That the whole group of ostracoderms was provided with a series of fringing plates similar to those of Cephalaspis is very probable, for a series of fringing plates are known to exist in Tremataspis, and I have found indications of fringing processes in the trunk of a fine specimen of Pterichthys preserved in the geological collection of McGill University.

Morphology of Vertebrate Appendages.— Organs so widely distributed in a primitive group of animals as the fringing processes are, must have great morphological significance. But while there is little doubt that they are the antecedents of the lateral fold of vertebrates, for no other structures so clearly reproduce in size, position and function the hypothetical folds from which the paired fins are supposed to take their origin, that fact does not help us to determine the morphological significance of the fringing plates themselves.

The fact that the fringing plates are marked with the same surface ornamentation as the trunk scales shows they are not comparable with internal fin rays. On the contrary, their ornamentation, shape, and mode of articulation indicate that they are independent, segmental structures. It is difficult to interpret such structures as anything else than appendages, having the same significance as the rudimentary abdominal appendages of arthropods.

Assuming that to be the case, we may form some idea of their probable mode of development by a comparison with those of Limulus. Miss Hazen and the writer have shown that here each abdominal appendage arises first as a fold of ectoderm, into which grows a muscle bud that soon divides into two principal parts to form the adductor and abductor muscles. Meantime the nerve to the appendage appears and an axial core of cartilage is formed which grows from the basal mesoderm through the middle of the muscle cells, toward the apex of the appendage.

As these processes agree in every essential particular with those known to occur in a segment of the lateral fold of vertebrates, there can be no serious objection, from an embryological standpoint, to the interpretation of the lateral fold as a series of fused abdominal appendages. Assuming then that the lateral fold is formed, phyllogenetically, by the fusion of a series of segmentally arranged, and independently movable structures, such as the fringing processes of the ostracoderms, it is clear that the oar-like cephalic appendages of the ostracoderms cannot be regarded as specializations of either a lateral fold, or of gill arches in the Gegenbaurian sense. On the contrary we must consider the paired cephalic appendages, gill arches and fringing processes as various modifications of one set of serially homologous structures, the pectoral and pelvic fins of modern vertebrates, being a comparatively recent specialization of a partially fused series of such appendages in the trunk region.

I assume, therefore, that the highly specialized condition of the visceral arches and appendicular structures of modern fishes arose through the modification of paired segmental appendages. Even in the more remote ancestors, such as the Phyllopoda, Trilobita, Phyllocarida and Merostommata. These appendages varied greatly in form and function in different animals, and in different regions of the body in the same animal.

In the ostracoderm type, we may assume that certain ones of the anterior cephalo-thoracic appendages were retained as oar-like swimming appendages. Two or three pairs were retained about the mouth followed by several pairs of respiratory appendages of an unknown character.

The trunk appendages were represented by the series of fringing processes.

We may assume that the evolution of the true vertebrates was accompanied by the fusion of the paired mouth parts into unpaired upper and lower jaws, by the further specialization of the gill pouches, the reduction of the free cephalic appendages to such embryonic structures as certain oral papiliæ or tentacles, external gills, and the larval balancing organs seen in certain amphibian larvæ, and by the fusion of the abdominal appendages to form the lateral fold from which in turn arose the pectoral and pelvic appendages.

The above interpretation of the origin of paired appendages retains the strong points of both the gill arch, and the lateral fold theories, without the weak points of either. It gives us precisely what Gegenbaur claims has heretofore been lacking in the lateral fold theory, namely: (1) a reason for the existence of the primary fold of ectoderm that initiates the formation of the lateral fold; (2) a reason for the migration into it of segmental detachments of muscle, nerve and cartilage; and (3) a primary function for the lateral fold out of which a set of locomotor organs could be logically developed.

We may explain the presence in the ostracoderms of two or more pairs of cephalic appendages that are not homologous with one another or with the pectoral fins, without being forced to assume that such highly specialized structures are nothing but movable spines or cornua, or flexible flaps, without any known antecedent function or significance. We may agree with Gegenbaur that there is a certain homology between gill arches and specialized portions of the lateral fold, without assuming the extensive migrations of gill arches demanded by his theory, and we may agree with Dohrn that structures homologous with gills, or associated with them, extended far back into the trunk region without assuming that true gill arches and visceral clefts were present there.

IV. MODE OF LIFE OF THE OSTRACODERMS. — We may form some idea of the mode of life of the Ostracodermata by considering the shape of the body and its armor, the nature of the appendages, and the position of the eyes and mouth.

That the Cephalaspidæ were sluggish animals is indicated not only by the clumsy shape, and large size of the heavily armored head, but also by the absence of an axial skeleton, and by the feeble development of the trunk and the dorsal and caudal fins.

The overlapping of the large scales on the dorsal surface of the trunk in Cephalaspis, and the presence of minute ventral scales, indicate some freedom of movement in a dorso-ventral direction and a restriction of those lateral movements so essential to sustained swimming when well developed appendages for that purpose are absent.

The dorsal fin was short and low and covered with close set scales that would allow but little freedom of movement.

The Cephalaspidæ, therefore, were in all probability bottom feeders. Any one that has watched Limuli, both old and young, ploughing slowly through the soft mud and sand, leaving little more than their median ocelli and lateral eyes exposed, could hardly avoid the conclusion that many of the trilobites and Cephalaspidæ, whose eyes are placed high up on the convex surface of similar shovel-shaped heads, must have moved about on the bottom in a similar manner.

But Limulus frequently crawls with considerable rapidity over the surface of shallow bottoms, or turning on its back with the aid of its caudal spine, even the largest and heaviest female may leave the bottom and swim slowly away with legs, operculum and gill covers beating the water in unison with oar-like strokes. The young larvæ, especially in the trilobite stage, swim very persistently in this inverted manner. It is also well known that Branchipus, Apus and many copepods swim in this position, and there can be but little doubt that many trilobites and merostommata did the same.

The Cephalaspidæ were certainly disproportionately heavy at the anterior end, so that any attempts to swim by movements of the trunk alone would tend to push the head deeper into the mud or sand, a tendency that would be increased by the sharp downward slope of the anterior dorsal surface. It is also probable, judging from the shape of the head and trunk, that its centre of gravity was situated above the mass centre, so that if the animal did succeed in getting off the bottom, it would have a

tendency to topple over and thus bring the ocular surface underneath. In this position, however, owing to the convexity of the surface, now underneath, any forward movement would tend to elevate the head and thus counteract the effect of its greater weight and volume.

When the Cephalaspidæ, therefore, left the bottom they probably turned over on to the ocular surface and made their swimming excursions in much the same manner as the above mentioned arthropods.

Whether the locomotion of the Cephalaspidæ was aided by the movements of branchial appendages concealed beneath the arching under surface of the head, can only be determined by the study of more perfect remains than have been as yet discovered. Certainly the very strongly concave under surface of the head indicates the presence there of some organs freely movable and of considerable size, projecting ventrally and laterally from the middle region of the head.

What we have said in regard to mode of life of the Cephalaspidæ will apply, with slight modifications to other members of the ostracoderms.

The Asterolepidæ, with their powerful, but badly constructed and impractical appendages and large centrally placed eyes, represent the extreme development of the free swimming type. It is quite certain that in some genera the attachment of the slender swimming appendages close to the ventral side, and the very highly arched dorsal surface, must have made it extremely difficult, if not impossible, for these animals to swim with the ocular, or dorsal surface, uppermost.

The methods of locomotion in the ostracoderms and the arthropods thus have a double value for they show us that animals like Limulus, the Phyllopoda and probably the Trilobita and the Merostommata, adopted when swimming a vertebrate position with the neural side uppermost, and that the ostracoderms must have frequently assumed the typical invertebrate position.

In Pteraspis, Cyathaspis and Tolypelepis, the lateral eyes are probably absent, or were covered with such thick layers of the shell as to render them nearly useless. The trioculate median eye, however, is well developed and is represented in Pteraspis

by a small pit on the under side of the dorsal shield, in Tolypelepis by an inconspicuous smooth spot on the outer surface, and in Cyathaspis by three obscure markings. These conditions indicate a considerable degeneration of the visual organs in these genera and must have profoundly modified their mode of life toward one of less activity and greater simplicity. We have here a condition approaching that of the lampreys, where the lateral eyes may be nearly functionless, while the median ones attain a degree of development that is hardly exceeded by that in any other vertebrate.

In Cephalaspis, the mouth was almost certainly situated high up on the vaulted under surface of the head and the character of the mandibles, as well as the small space into which such organs must have been crowded indicates that the mouth was very small. Similar conditions prevailed in Tremataspis, Bothriolepis and other members of the ostracoderms. Under these conditions and with their necessarily slow and clumsy movements, the ostracoderms could not have been rapacious animals. The position of their eyes, whether well developed or not, points with equal decisiveness to the same conclusion, for whether swimming or crawling, they could not see where, or when, to seize their prey, because their eyes would always be behind their own body. They must have been dependent on highly specialized gustatory, or tactile, organs situated near the mouth.

As a parasitic life for such animals is out of the question, it is probable that they lived on the soft bodied animals or decomposing organic matter that could be exposed or forced into the mouth as they slowly ploughed their way through the soft mud or sand.

Dartmouth College, Hanover, N. H.
July 10, 1903.

PLATE I.

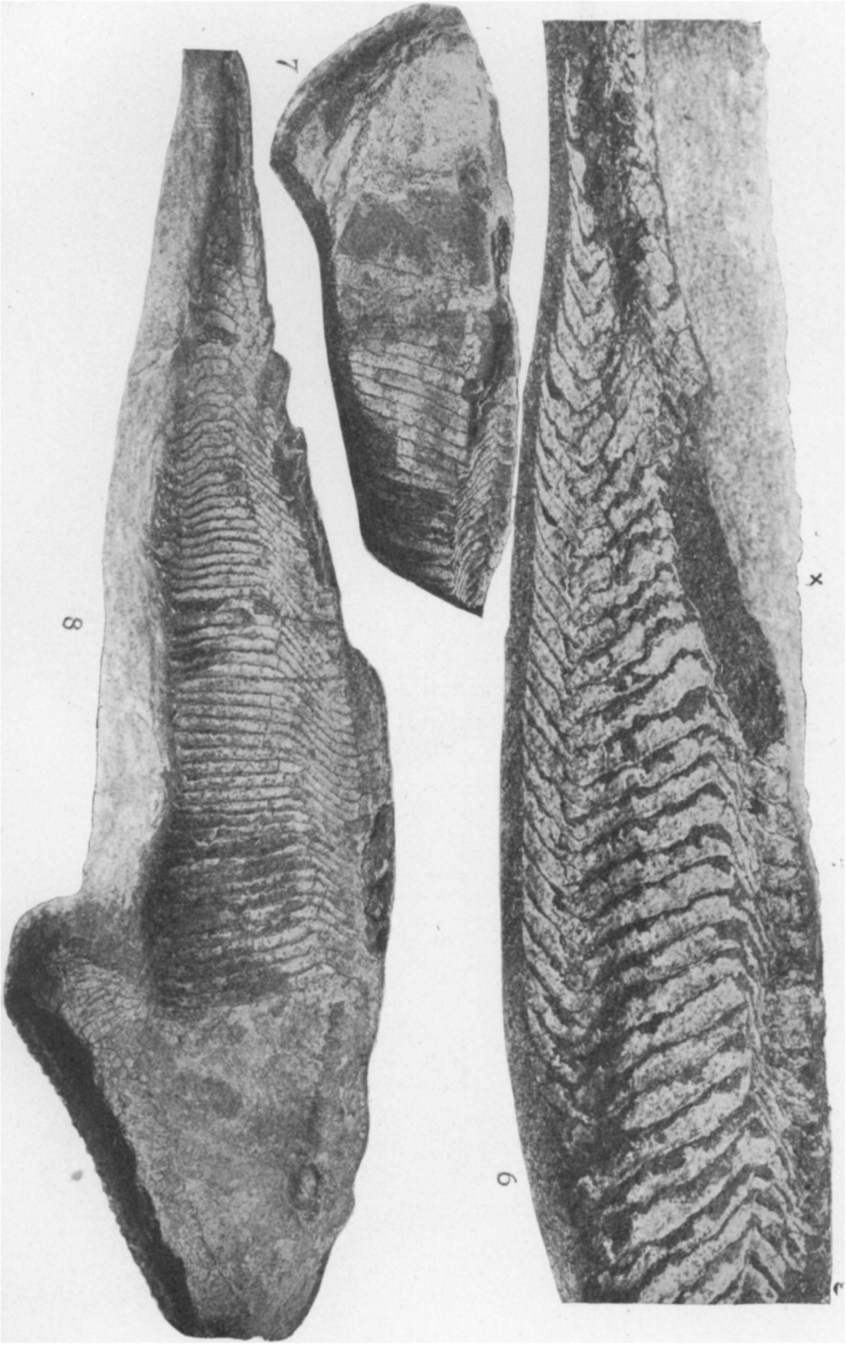


PLATE II.

Explanation of Plates.

PLATE I.

Fig. 1.—*Cephalaspis murchisoni*, showing several lobed fringing processes, *fp*. British Museum.

Fig. 2.— Head of Cephalaspis. Outer layers of the shell are absent, showing outlines of the bony trabeculæ below the lateral openings and the post-orbital valley.

Fig. 3.— Shows outline of the lateral openings filled with polygonal plates. British Museum.

Fig. 4.— Shows the impressions of radiating blood vessels on the inner surface of the shield. British Museum.

Fig. 5.— Ventral surface of the trunk of Cephalaspis, showing the cloacal opening.

PLATE II.

Fig. 6.— Side view of the trunk of *Cephalaspis lyellii*, showing the fringing processes and their articulation with the lateral trunk scales. British Museum.

Fig. 7.— Head and anterior portion of the trunk of Cephalaspis, showing arrangement of the trunk scales. British Museum.

Fig. 8.— Side view of head and trunk of *Cephalaspis murchisoni*. British Museum.

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